

1       **Ecological theory of mutualism: Qualitative patterns in two-species population models**

2                               Kayla R. S. Hale<sup>1\*</sup> & Fernanda S. Valdovinos<sup>2\*</sup>

3       <sup>1</sup> Department of Ecology and Evolutionary Biology, University of Michigan, Biological Sciences  
4       Building, 1105 North University Ave, Ann Arbor, MI 48109, USA.

5       *Email:* [kaylasal@umich.edu](mailto:kaylasal@umich.edu)       *Phone:* [+1 \(989\) 770-6618](tel:+19897706618)

6       <sup>2</sup> Department of Environmental Science and Policy, University of California, Davis, Wickson  
7       Hall, One Shields Avenue, Davis, CA 95616.

8       *Email:* [fvaldovinos@ucdavis.edu](mailto:fvaldovinos@ucdavis.edu)       *Phone:* [+1 530-754-2383](tel:+15307542383)

9       \*Corresponding authors

10      *Keywords:* density-independence, density-dependence, cost-benefit, consumer-resource,  
11      dynamics, stability, functional response, thresholds, Allee effect, overexploitation

12      *Manuscript type:* Synthesis

13      *Running title:* Ecological theory of mutualism

14      *Word count:* Abstract: 169 / 200 Main text: 7291 / 7500

15      *Number of references:* 100

16      *Manuscript elements:* Figures 1-4, Tables 1-2

17      *Acknowledgements:* This research was supported by National Science Foundation Graduate  
18      Research Fellowship DGE-1143953 to K.R.S.H. and National Science Foundation grant DEB-  
19      1834497 to F.S.V.

20      *Competing interests:* The authors declare no competing interests.

21      *Statement of authorship:* F.S.V. conceived and conceptualized the study. K.R.S.H. and F.S.V.  
22      conducted literature review. K.R.S.H. analyzed the models and wrote the first draft of the  
23      manuscript. F.S.V. and K.R.S.H. developed the conclusions and revised the manuscript.

- 24 *Data accessibility:* No new data were used in this work.
- 25 *Code availability:* Mathematica notebooks used to analyze models and generate figures will be
- 26 available on GitHub upon acceptance.

## Abstract

Mutualisms are ubiquitous in nature, provide important ecosystem services, and involve many species of interest for conservation. Theoretical progress on the population dynamics of mutualistic interactions, however, has comparatively lagged behind that of trophic and competitive interactions. Consequently, ecologists still lack a generalized framework to investigate the population dynamics of mutualisms. Here, we review historical models of two-species mutualisms from over the last 90 years. We find that population dynamics of mutualisms are qualitatively robust across derivations, including levels of detail, types of benefit, and inspiring systems. Specifically, mutualisms exhibit stable coexistence at high density and destabilizing thresholds at low density. We distinguish between thresholds resulting from Allee effects, low partner density, and high partner density, and their mathematical and conceptual causes. The dynamics of stable coexistence and thresholds in partner density emerge when benefits of mutualism saturate, whether due to intrinsic or extrinsic density dependence in intraspecific, interspecific, or both. These results suggest that there exists a robust population dynamic theory of mutualism that can make general predictions.

## Introduction

Mutualisms are ubiquitous in nature and serve indispensable roles in supporting biodiversity and ecosystem function. Nearly all species on Earth participate in at least one of four main types of mutualism: seed dispersal, pollination, protection, and resource exchange including with symbionts (Janzen 1985, Bronstein 2015a,b). Moreover, up to  $\sim 3/4$  of phosphorus and nitrogen acquired by plants is provided by mycorrhizal fungi and nitrogen-fixing bacteria (van der Heijden *et al.* 2008) and  $\sim 1/3$  of crop production is dependent on animal pollination (Klein *et al.* 2007). The last 40 years has seen an important increase in studies on population ecology of mutualism but with little representation in textbooks (e.g., Kot 2001, Turchin 2003, Gotelli 2008, Morin 2011, Vandermeer & Goldberg 2013, Mittlebach & McGuill 2019; but see McCann & Gellner 2020 for a chapter on mutualistic networks) and recent syntheses of theoretical ecology (e.g., Hastings & Gross 2019). This is, perhaps, due to disparate approaches and terminologies within this literature, on which we elaborate below. However, the qualitative predictions of this body of work are coherent and robust, and we submit that ecology will benefit from recognizing them as such. To make this ecological theory of mutualism available to the broader ecological community, we review the historical literature on the ecological theory of mutualism and synthesize generalities, both mathematical and conceptual, that can lay a foundation for deeper understanding of mutualism and, possibly, of community ecology as a whole.

Foundational theory in ecology was initially developed using Lotka-Volterra models. In this framework, constant coefficients describe the positive or negative effects between two interacting species as a linear function of the other species' density. The Lotka-Volterra model for predation and competition predict stable cycles (oscillations, Lotka 1925, Volterra 1926) and competitive exclusion (Volterra 1926, Gause 1934), respectively, which stimulated fruitful



empirical and theoretical work. Indeed, from the groundwork of Lotka-Volterra theory of predation came more general consumer-resource theory, with useful and surprising results such as the paradox of enrichment (Rosenzweig 1971) and a mathematical representation of seasonal cycling in lake food webs (Boit *et al.* 2012).

In contrast, Lotka-Volterra models for mutualism have been a less useful simplification than for predation and competition (Holland 2015). The original model (Gause & Witt 1935) and other formulations in which species benefit as a linear function of each other's density (Addicott 1981) can predict unbounded population growth of both species (famously, "the orgy of mutual benefaction," May 1976). Additionally, the diversity of mechanisms by which species may benefit each other and the non-reciprocity of many of them, has cast suspicion on representing any "mutualistic" interaction as a simple exchange of positive effects (Bronstein 2001a,b). Mutualisms are more likely to exhibit shifting net effects than other interaction types (Chamberlain *et al.* 2014, Jones *et al.* 2015), with several exchanges dipping, for example, into parasitism.

Despite all these interesting mechanisms and patterns ripe for study, mutualisms have been subjected to less theoretical study than predation and competition. Many have speculated on historical reasons (Boucher 1985, Bronstein 2015b, Raerinne 2020), but we highlight two here. First, the terms used to identify interactions as "mutualism" have changed over time. Previous theory treated mutualism as a subset of facilitation, in which one species alters the environment to benefit a neighboring species (Callaway 2007), or symbiosis, in which species coexist in "prolonged physical intimacy" (Bronstein 2015b), or used those terms interchangeably. Additionally, the terms "mutualism," "cooperation," and "protocooperation" have been used idiosyncratically for beneficial interactions within species as well as between them (Bronstein

2015b). Furthermore, some mutualisms are “indirect,” such that benefits to one partner can only be realized in the presence of an external species or environmental condition (Holland & DeAngelis 2010). In this review, we limit our scope to mutualism defined as reciprocally beneficial interactions between two species without reference to the partners’ intimacy or environmental effects (Bronstein 2015b). We largely focus on direct mutualism or models that approximate the effects of indirect mutualism through two-species models, though we touch on some other cases (e.g., Thompson *et al.* 2006).

Second, the mechanisms by which species benefit each other in mutualisms are extremely diverse. These mechanisms include, but are not limited to, habitat provisioning, deterrence of predators or competitors, increased growth, faster maturation, facilitated reproduction, improved digestion, parasite grooming, and resource consumption. Conceptual frameworks have attempted to organize this rich diversity, for example, by the types of benefits exchanged (nutrition, protection, or transportation), the mechanisms of exchange, or the obligacy of each partner (reviewed in Bronstein 2015, Douglas 2015). This diversity of mechanisms makes the development of general but informative theory for mutualism more difficult than, for example, predator-prey theory, in which the interaction can be simply modeled as the consumption of individuals of one species by the individuals of the other species.

As it stands now, mutualism has repeatedly been called a loose set of natural history studies with little theory to unite or divide them (Addicott 1981, Bronstein 2015). Despite an increasing number of theoretical studies, an “ecological theory of mutualism” has not penetrated the greater ecological community (Bronstein 2015, Valdovinos 2019, recent textbooks). The studies that exist have suffered from a pattern of neglect and repeated rediscovery (Boucher 1985, Morin 2011). Calls continue for simple but usable theory that synthesizes among

mutualisms to identify patterns in population dynamics and in the mechanisms that generate them (e.g., Addicott 1981, Bronstein 1994, Bronstein 2001, Callaway 2007, Bronstein 2015a). Here, we review ecological theory of mutualism, highlighting many now-obscure texts that have contributed to the field's current understanding. We focus exclusively on ecological models, leaving other aspects of historical mutualism research including game theory and biological market models to previous (excellent) sources (Hoeksema & Bruna 2000, Bronstein 2015). Additionally, we focus on the bulk of theory that conforms to the typical assumptions of population dynamic approaches (Gotelli 2008). That is, we focus on continuous-time models without immigration or emigration (i.e., closed systems), without age, stage, or genetic structure, and under the approximation that individuals encounter each other randomly with no spatial structure (mean field assumption). We use phase plane diagrams (Figs. 1-4) to visualize the different qualitative dynamics of these models, as determined by species' curves of zero growth ("nullclines") and fixed points ("equilibria") of the system. We organize the development of the theoretical study of mutualism by its historical focus on the form of benefit either as linearly increasing with partner density or limited by intraspecific or interspecific density-dependence, and its more recent incorporation into consumer-resource theory (Table 1).

After reviewing this rich and often overlooked body of work on the ecology of mutualism, we identify patterns in the predictions of these models that stand across systems and assumptions. We argue that extant models make a robust set of qualitative predictions and that these predictions qualify as an ecological theory of mutualism.

## Historical Review

### *Linear benefit models*

Gause and Witt (1935) proposed a model for mutual aid between a host and symbiont, inspired by Konstitzin (1934; Wolin 1985). This model was a modification of the Lotka-Volterra competition equations with positive (instead of negative) interaction coefficients (Eqn 1; see Table 2 for numbered equations). Benefits increased linearly with increasing partner density, while the strength of negative (intraspecific) density-dependence also increased linearly with the growth of the species receiving the benefit (i.e., the recipient species; Fig. 1B-F). In this formulation, mutualism has two effects: it increases the low-density growth rate of the recipient and the recipient's "equilibrium" density. The second effect means that mutualism increases the carrying capacity of the recipient species in the presence of its partner. However, hereafter, we reserve the term carrying capacity for density in the absence of the mutualistic partner. As written, the model accommodates only what we now call "facultative" mutualists (Vandermeer & Boucher 1978), those that can persist at positive density ("carrying capacity",  $K$ ) in the absence of their partner ( $K > 0$ ). Gause and Witt also commented that increasing the coefficients of mutual aid increases both species' equilibrium biomass until they pass to infinity, but that infinite populations are obviously unreasonable and microcosm studies suggest that the strength of mutual aid coefficients should decrease as species grow. These two studies (i.e., Konstitzin 1934, Gause & Witt 1935) initiated theoretical research on what we now call mutualism around the same time as theoretical research on predation and competition, but then paused for nearly 40 years (until 1970s).

Beginning in the 1970s, mutualism received attention as a destabilizing force in ecological networks represented as random community matrices (May 1972, May 1973), with the unbounded growth in the Lotka-Volterra models of mutualism being called a "silly solution" that leads to an "orgy of mutual benefaction" (May 1976). Using Lotka-Volterra models, authors

157 better characterized the conditions that lead to unbounded growth found by Gause and Witt's  
158 original model of mutualism (Albrecht *et al.* 1974, Vandermeer & Boucher 1978, Goh 1979,  
159 Travis & Post 1979). Other forms of linear benefits were investigated such as those that increase  
160 per-capita growth rate, equilibrium density, or both (Fig. 1). Whittaker (1975) introduced a  
161 model in which mutualism increases the equilibrium density of one partner and both the  
162 equilibrium density and per-capita growth rate of the other partner. This model accommodates  
163 “obligate” mutualists like symbionts living on a host that cannot persist in the absence of that  
164 host, that is, have zero carrying capacity ( $K = 0$ ) in the absence of their partners. The mutualistic  
165 symbiont-host interaction linearly increases the carrying capacity for the symbiont (Eqn 2) while  
166 benefiting the host population by increasing its low-density growth rate and its equilibrium  
167 density (Eqn 1). Later, Addicott (1981) introduced a model in which mutualism only increases  
168 the per-capita growth rate (Fig. 1A, Eqn 4), inspired by the ant-aphid mutualism described in  
169 Addicott (1979). Addicott emphasized that these different linear benefit models could be used in  
170 a mix-and-match style to accommodate different types of benefits exchanges.

171 Vandermeer and Boucher (1978) proposed the groundbreaking idea that mutualistic partners  
172 may exist along continuums of obligacy and interaction strength. The authors defined facultative  
173 mutualists as those with positive carrying capacity in absence of their partner. Obligate  
174 mutualists were defined more abstractly with zero or negative carrying capacity in absence of  
175 their partner ( $K \leq 0$ ), which represents the demographic drawdown that mutualism must exceed  
176 to allow persistence of the population. Negative carrying capacity arises mathematically when a  
177 population has a negative “intrinsic” growth rate, as is the case when its per-capita death rate  
178 exceeds its per-capita birth rate (Table 2). This choice is useful both mathematically and  
179 ecologically because it allows the strong demographic pulldown when death rates exceed birth

rates to be represented, without introducing numerical issues due to zero carrying capacity. Vandermeer and Boucher's analysis of Gause and Witt (1935)'s model found that obligate partnerships would either collapse to extinction when benefits are weak or exhibit a threshold population size under which they go extinct and above which they grow unboundedly when benefits are strong (Fig. 1E-F). They also found that facultative partners are likely to coexist stably when benefits are weak or exhibit unbounded growth when benefits are strong (Fig. 1C-D, also see Wolin 1985). Remarkably, Vandermeer and Boucher (1978; also see Christiansen & Fenchel 1977) anticipated the qualitative dynamics generated by extending these models to saturating benefit responses. However, the authors emphasized that unbounded growth was still an ecologically relevant result because it indicates persistence of the two-species mutualistic system. Indeed, they argue that persistence (whether species persist or go extinct) is a more biologically useful metric than neighborhood stability (whether the system returns to equilibrium after a small perturbation). Subsequent authors also emphasized other properties of stability of mutualism such as return time to equilibrium (Addicott 1981, Wolin 1985), species persistence (Valdovinos *et al.* 2013, 2016, 2018), or biomass variability (Hale *et al.* 2020).

#### *Saturating benefit models*

The earliest models that incorporated saturating benefits within mutualism invoked unspecified (intraspecific) environmental constraints that limit population growth in the presence of a mutualist (Whittaker 1975, May 1976, Dean 1983, Wolin & Lawlor 1984). For example, Whittaker (1975) assumed extrinsic, intraspecific limiting factors to the benefits a host could receive from its symbiont (Eqn 3, Fig. 2A). This is the first of many models that exhibit thresholds (*sensu* Vandermeer & Boucher 1978), where the low density of one partner pushes the whole system to collapse. Some authors refer to these dynamics as "Allee thresholds" (e.g.,

Johnson & Amarasekare 2013), but these are not strictly Allee effects where populations decline due to their own low density.

This focus on extrinsic limits to benefit was epitomized by Wolin and Lawlor (1984). They derived models for five different ways in which mutualism could affect per-capita birth or death rates as functions of recipient density. For example, they compared models in which mutualism reduces intraspecific density-dependent limiting factors only in per-capita birth rates (Eqn 6, Fig. 2C-D), only in per-capita birth rate but with saturating effects (Eqn 5, Fig. 2B), and both in birth and death rates with saturating effects (Eqn 2, Fig. 1B). These models were classified as describing mutualisms with effects primarily at high versus low self-density. Wolin and Lawlor concluded that low-density effects (i.e., primary effects on per-capita growth rate as opposed to equilibrium density) are stabilizing in terms of faster return times and the existence of a feasible, stable equilibrium. These models of “intraspecific density-dependence” (so called by later authors, Holland 2015) lacked biological mechanisms or reference to clear ecological examples, which perhaps pivoted the field away from this otherwise fruitful approach. In contrast, Soberón and Martinez del Rio (1981) proposed a detailed pollination model in which plant benefits are a function of pollinators’ visitation rate, modeled as a saturating Type II functional response. Thus, benefits to plants saturate as a function of their own density (intraspecific density-dependence), but due to factors intrinsic to the mutualism (that is, time constraints for pollinators handling flowers during foraging visits). Such an approach has seen a resurgence in recent literature (see *Consumer-resource models*, below) but was largely abandoned at the time.

Starting in the late 1980s, authors began to focus on “interspecific density-dependence,” which has been considered more consistent with other theories of interspecific interactions (Holland 2015). Wright (1989) proposed a model in which per-capita benefits saturate in terms

of partner density analogously to consumers foraging on resources due to limitations of consumer handling of resources or uptake rate (Fig. 2E-F). In the mutualistic case, benefits are assumed to saturate with increasing partner density, often as an additive, first order term to per-capita growth rate following a Holling Type II functional-response (Wright 1989, Bazykin *et al.* 1997, Thompson *et al.* 2006, Holland & DeAngelis 2010, Wu *et al.* 2019, Hale *et al.* 2021). On the other hand, Thompson *et al.* (2006) proposed a theoretical framework that organized both terrestrial and aquatic mutualisms into those that affect birth rate, death rate, habitat acquisition or a combination of these benefits for each partner. Other authors have used different mathematical forms for analytical tractability (Pierce & Young 1986, García-Algarra *et al.* 2014). Regardless, these assumptions result in both an increase in low-density growth rate and an increase in equilibrium density in the presence of mutualists.

These studies using the interspecific density-dependence approach included more ecological justification for mechanisms that limited benefit accrual. However, phenomenological accounts of environmental conditions limiting population growth were still present with most models via an undiscussed intraspecific limitation term (see discussion by Johnson & Amarasekare 2013). That is, authors assumed that at least one partner was limited by negative density-dependence to ensure curved nullclines and stable coexistence in the mutualism. Recently, Moore *et al.* (2018) introduced nonlinearities in intraspecific limitation while maintaining linear benefits. Mutualism is stable when density-dependence accelerates with increasing recipient density. Ecologically, this means that the growth rate of the population receiving the benefit decreases faster and faster at higher density, which has been observed empirically (Moore *et al.* 2018). This result highlights the importance of investigating the effect



of more realism in intraspecific limitation on the dynamics of mutualism, which has been largely under-explored.

Other authors derived models with benefits limited by both inter- and intraspecific density-dependence (May 1976, May 1978, Wells 1983, Fishman & Hadany 2010, Johnson & Amarasekare 2013). This added complexity was usually justified by system-specific considerations (e.g., May 1976, Wells 1983), but it also emerges from individual-level mechanisms in plant-pollinator systems (Fishman & Hadany 2010) or intraspecific competition for food or services (Johnson & Amarasekare 2013). In general, these limitations emerge when systems are limited both by availability of service providers (e.g., pollinators) and by the substrates that receive benefit (e.g., flowers to be pollinated, seeds to germinate, or individuals to protect from predators; Hale *et al.* 2021).

#### *Cost-benefit models & shifting net effects*

A blooming of empirical work that started in the 1980s revealed that mutualisms are not only more (omni)present than previously expected but also context-dependent (Thompson 1988, Bronstein 1994, Herre *et al.* 1999, Chamberlain *et al.* 2014). That is, the effect of these interactions often shifts between mutualism and parasitism or competition due to the relative balance of costs and benefits of participating in the interaction. Moreover, costs and benefits themselves may be strongly varying across space, time, and other abiotic conditions. Early investigations of this topic used models that could accommodate different types of interactions through smooth transitions in parameter values (Whittaker 1975, Pierce & Young 1986). For example, Pierce and Young (1986) do not provide a specific mathematical form but use a geometric argument to investigate the dynamics of an ant-lycaenid butterfly interaction in which lycaenids may be mutualistic, commensalistic, or parasitic to tending ants.

Neuhauser and Fargione (2004) explored the mutualism-parasitism continuum using the classical predator-prey (or host-parasite) Lotka-Volterra model with the additional possibility of the parasite benefiting the host (Fig. 3A-B). The model includes both benefits and costs and it was applied to study plant-mycorrhizae interactions across gradients of soil fertility. The authors assumed that mycorrhizal fungi increase host-plant equilibrium density (benefits) but also linearly increase plant death rate due to exploitation (costs). This and other cost-benefit models can exhibit coexistence equilibria that are stable spirals, meaning that the populations densities will oscillate towards a fixed point (see *Patterns from Theory*). Zhang (2003) also modified a Lotka-Volterra model to accommodate mutualism but chose the competition instead of the predator-prey version of the model (Fig. 3C-E). The modified model assumed that the interaction between species was competitive at high density and mutualistic at low density, modeled phenomenologically as parabolic nullclines. This model can predict competitive exclusion, competitive coexistence where one partner dominates depending on initial density, thresholds in which low density of one partner drives the system to collapse, or “mutualism” according to the criterion that species coexistence stably at higher density than either could have achieved alone. Unfortunately, it is difficult to understand which of the diverse dynamics this model can exhibit are most ecologically relevant because interpretation is not provided for its parameters. A mechanistic derivation that achieves similar dynamics could be useful future work (but also see Gross 2008 for a similar approach on an explicit resource).

Other models also described different outcomes depending upon relative species' density (Hernandez 1998, Holland *et al.* 2002, Wang *et al.* 2019). In an important advance, Holland *et al.* (2002) proposed a suite of models in which different net effects result from the difference between increasing benefit functions and linear, saturating, or decreasing cost functions (see Fig.

1 of Holland *et al.* 2002). Their approach balances out different mechanisms that cause net effects of the interaction to shift as the relative densities of the populations change over time.

In seeking to represent the phenomena or mechanisms of shifting interaction outcomes, cost-benefit models revealed a much more complex set of potential dynamics for mutualism than had been previously reported. Saturating costs bends species' nullcline towards the partner's axis at high partner density, curving it back around towards the origin into a lobe shape (Fig. 3C-G). This is because high partner density exerts high saturating costs on the recipient due to resource consumption, which may exceed the benefits that can be acquired. Up to five non-trivial equilibria occur when coexistence is feasible. Moreover, separatrices running through saddle points define basins of attraction that lead to extinction or potential single-species persistence for facultative species. This ensures instability when one population is of substantially higher density than the other due to overexploitation of the rare partner (Fig. 4B). These dynamics contrast with the threshold effects (Fig. 4A) wherein the low-density partner benefits from mutualism but cannot provide sufficient reciprocal services. When the low-density partner becomes even rarer, it experiences an Allee effect, leading to its extinction (Fig. 4B). The high-density partner will also go extinct if it is obligate upon the low-density partner.

This much more complex set of potential dynamics that emerges from cost-benefit models exemplifies the criticism to mutualism theory as either too system-specific or too abstract to provide general insight into patterns and processes in mutualism (Bronstein 2001, Holland 2015). Additionally, the field had not clearly connected the costs and benefits observed for individuals participating in a mutualism to potential population-level effects. The time was ripe for a conceptual synthesis.

*Consumer-resource approach to mutualistic interactions*

In a landmark work, Holland and DeAngelis (2010) formalized a consumer-resource approach to mutualism, providing a bridge between mutualism and the ecology of other interspecific interactions. In their framework, mutualisms may be “unidirectional” or “bidirectional” consumer-resource interactions, in which one or both partners benefit from consuming costly resources provided by the other (Fig. 4B, Fig. 3F-G, respectively). Such framework accommodated the shifting net effects of previous models (Holland & DeAngelis 2009, previous section), and formalized the concept of ecological costs and benefits as modifications to demographic rates due to resource provisioning and nutrient or service consumption. Notably, this framework allowed mutualisms to be modeled as a dynamic continuum along a spectrum of other interspecific interactions, such as predator-prey and competitive interactions (Holland & DeAngelis 2009, Holland 2015). This was possible by clarifying the “currency” of the effects of mutualism as energy or biomass exchanges that manifest in changes to per-capita growth rate (or its components: birth, death, immigration, etc.). This framework stimulated recent development of theory for more specific systems (e.g., Kang *et al.* 2011, Martignoni *et al.* 2020)

Holland and DeAngelis (2010) modeled specific study cases similarly to previous studies (see *Saturating benefits* section), but with costs defined separately from benefits via saturating interspecific functions, accrued through provisioning resources. In contrast, service-provisioning by consumers is assumed to incur only fixed costs that can be accounted for in parameter values, like increased handling time when foraging for resources. The nonlinear costs cause lobe-shaped nullclines allowing up to five coexistence equilibria. Like the earlier Zhang (2003) model, many dynamics are possible including mutualistic stable coexistence and oscillations. However, instead of the competitive exclusion and competitive coexistence outcomes of Zhang’s model,

“parasitism” by one partner is due to exploitation by a high-density partner that outweighs the benefits it provides to the lower density partner. In most dynamics of the Holland and DeAngelis’ model, parasitism collapses the system to extinction instead of allowing a stable but exploitative interaction like in Zhang’s model.

Valdovinos *et al.* (2013) proposed a new type of consumer-resource model in which consumption is on “rewards” rather than individuals of the resource population directly (but also see Scheuring 1992 for a similar stage-structured model). Rewards are resources provided by one species to attract their mutualistic partners (Bronstein 2009). This model separates the dynamics of the plants’ vegetative biomass from the dynamics of the plants’ floral rewards. This key separation allows one to (1) track the depletion of floral rewards by pollinator consumption, (2) evaluate exploitative competition among pollinator species consuming the floral rewards provided by the same plant species, and (3) incorporate the capability of pollinators (adaptive foraging) to behaviorally increase their foraging effort on the plant species in their diet with more floral rewards available. Another advance of this model is incorporating the dilution of conspecific pollen carried by pollinators, which allows tracking competition among plant species for the quality of pollinator visits (see the next section). This model was developed for plant-pollinator networks, but its ideas paved the way for new investigations of mutualism at the pairwise (Revilla 2015, Wang 2019, Hale *et al.* 2021) and community (Valdovinos *et al.* 2016, Valdovinos & Marsland 2021, Hale *et al.* 2020) scales. For example, Revilla (2015) assumed rewards achieve steady state compared to changes in population density and derived models in which the linear consumption rate on rewards mediates benefits to the resource species. Hale *et al.* (2020) considered that pollinator visits can be approximated by consumption of floral rewards, and assumed that benefit to both plant and pollinator species is proportional to

consumption rates on floral rewards. Hale *et al.* (2021) further specified whether benefits should be proportional to per-capita consumption rate (as may be the case for animal-dispersed plants) or to total consumption rate (as may be the case for animal-pollinated plants which require obligate outcrossing). The latter leads to emergent Allee effects (Courchamp *et al.* 2018) for obligately animal-pollinated plants, explained by the plants' inability to attract pollinators at low density.

### Patterns from Theory

We found that predictions for the population dynamics of mutualisms are qualitatively robust across the models reviewed, despite differences in level of detail, types of benefit, and inspiring systems. We synthesize these general findings below.

#### *Mutualisms are stable with self-limitation and saturating benefits*

The stability of mutualistic interactions has generated controversy in the community ecology literature for decades (May 1972, May 1973, Bascompte *et al.* 2006, Holland & DeAngelis 2010, Allesina & Tang 2012, Johnson & Amarasekare 2013, Holland 2015, Valdovinos 2019, Hale *et al.* 2020). Topics of debate include definitions of stability (e.g., lack of positive feedbacks, robustness to perturbations), the scale at which they are assessed (e.g., pairwise interactions, between guilds, within communities), and stabilizing mechanisms (e.g., non-random interactions, environmental limits, consumer-resource dynamics).

Despite this debate, we found that theoretical investigation of pairwise mutualism has become conclusive: mutualisms are stable. Minimal realism in terms of limited benefits, accumulating costs, or accelerating intraspecific competition allow stable coexistence at high density according to the criteria of local stability analysis. That is, these systems will return to equilibrium after small perturbations to population densities. Under other definitions of stability,

such as persistence of populations or return time to equilibrium, mutualisms can be even more stable than predation and competition (Addicott 1981, Wolin & Lawlor 1984). Moreover, other mechanisms not reviewed here including spatial structure (Armstrong 1987, Amarasekare 2004, Mohammed *et al.* 2018), rewards or resource dynamics (Meyer *et al.* 1975, Scheuring 1992, Gross 2008, Revilla 2015, Cropp & Norbury 2019, Wang 2019), adaptive foraging (Valdovinos 2013, 2016, 2018) and predators or competitors (Heithaus *et al.* 1980, Addicott & Freedman 1984, Ringel *et al.* 1996, Mougi & Kondoh 2012, Hale *et al.* 2020) also stabilize mutualisms.

The pattern of stable coexistence of mutualists at high density is robust across mechanisms that limit benefit (Figs. 2-3). Both inter- and intraspecific density dependence lead to the same qualitative dynamics when they are present in at least one partner (also see *Thresholds*, below). One exception can occur when benefits accrue directly to a term that represents intraspecific density-dependence, which decreases per-capita growth rate at high density. If mutualism decreases this negative density-dependence to such an extent that it induces positive density-dependence at high partner density, the recipient population will begin accruing increasing benefit with its own increasing density (e.g., Eqns 5, 20). Then, the system can display unbounded growth (Fig. 2C-D) unless there are additional external limits to benefits accrued (Fig. 3K).

### *Mutualisms exhibit thresholds when at least one partner is obligate*

Nearly all models that predict stable coexistence at high density also predict destabilizing thresholds at low density when one or more partners are obligate upon the mutualism (Fig. 2, Fig. 3A-B, H-K). Specifically, if either species dips below a critical threshold in population density, the obligate partner(s) will go extinct, even if initially at high density (Fig. 4A). This collapse occurs because, under the threshold, the low-density species cannot provide sufficient

benefits to its higher density partner. Threshold effects occur in systems with interaction strengths high enough to allow feasible coexistence, but with per-capita growth rates small enough (very negative for obligate partners, near-zero for facultative partners) that a partner can potentially achieve densities low enough for long enough that its obligate partner will go extinct.

Understanding threshold dynamics provides rich insight into interaction strength, obligacy, and positive feedbacks in mutualistic interaction. By definition, obligate mutualists have negative per-capita growth rate or carrying capacity in the absence of their partner. Thus, obligate mutualists can be only saved from population decline by benefits from mutualism that exceed their own negative intrinsic growth rate, that is, via strong mutualistic interactions. If both partners are initially at high enough density, obligate mutualists can achieve positive population growth, resulting in stable coexistence. However, if an obligate mutualist is at high density but its partner is at low density, the obligate mutualist will decline quickly due both to its negative intrinsic growth rate and due to strong intraspecific limitation at high density. The low-density partner may be growing due to mutualistic benefits, positive intrinsic growth, or release from intraspecific limitation. However, under the threshold, its population cannot recover fast enough to provide sufficient benefit to cancel out the negative intrinsic growth rate of the obligate partner and save it from decline. On the other hand, facultative partners can rely upon their own positive intrinsic growth rate to recover from low density, even after declines due to strong intraspecific competition or insufficient benefits provided by its partner. Thus, threshold effects do not occur in facultative partnerships.

These threshold dynamics emerge from the unique nature of mutualism and are potentially characteristic of this interaction. In predator-prey interactions, a low-density predator may benefit from a higher density prey population that is declining, but negative feedback in the



system also allows the crash of the predator population at high density and subsequent recovery of the prey population. In competition interactions, the higher density partner exerts stronger and stronger negative effects on the rare population, causing the rarer population to go extinct. In contrast, the positive feedback in the mutualistic system requires that both partners can provide sufficient benefits to the other to maintain the interaction. Notably, thresholds effects also occur in models that take very different approaches than those reviewed here. For example, Ingvarsson & Lundberg (1995) observed threshold effects dependent upon the ability for pollinators' ability to find flowers in a modified disease model for mutualism, while Wang (2019) showed that the thresholds observed in Revilla's (2015) model more precisely occur between pollinator and rewards density rather than pollinator and plant density directly. This further emphasizes the potential generality of thresholds in mutualisms.

#### **Allee Effects**

Allee effects are another form of threshold but where the population declines below a threshold of its own density (instead of the partner's density). Here, we use "Allee effects" to refer specifically to strong, demographic Allee effects (Kramer *et al.* 2009) that emerge from the mutualism (i.e., are not hard coded into the population dynamics, Courchamp *et al.* 2018). Allee effects have been observed in food chains that include protection mutualism (Morales *et al.* 2008) and in models of sequential colonization of patches by plants and mobile mutualists (Amarasekare 2004). As mentioned above, Hale *et al.* (2021) finds Allee effects in obligate plants when they become too rare to attract sufficient visitation from pollinators (Fig. 4C). Holland & DeAngelis (2010) find Allee effects in animal populations induced by overexploitation from another consumer mutualist.

454                    *Strong interactions are needed for obligate mutualists to persist*

455                    Research on mutualistic interactions has yet to firmly define interaction strength  
456 (Valdovinos 2019). In Lotka-Volterra models, interaction strength is simply defined by the  
457 benefit coefficient ( $\alpha_{ij}$  in Eqns 1, 2, 4). However, as authors have gained deeper mechanistic  
458 understanding of mutualism, it has become clear that interaction strength is a more complex  
459 topic related to the “effectiveness” of mutualistic partners (Vazquez *et al.* 2015, Schupp *et al.*  
460 2017). Schupp *et al.* defined the effectiveness of a population for providing mutualistic benefits  
461 to its partner as the product of the “quantity” and “quality” of benefits provided. The term  
462 “quality” accounts for the species-specific and interaction-specific traits, as well as the  
463 environmental context that determine how much benefit a partner can receive from a unit of  
464 benefit “quantity”. Examples of such benefit quality are the nutrition acquired from a foraging  
465 visit or the probability of a seed recruiting after being removed by a disperser.

466                    The parameters that determine the quality of the mutualistic interaction are useful for  
467 understanding the criteria for stable coexistence and thresholds. Weak interactions between  
468 facultative partners in Lotka-Volterra models are considered stabilizing because they ensure  
469 stable coexistence instead of permitting unbounded growth. Specifically, mutual benefits must be  
470 weaker than species’ intraspecific limitation (Gause & Witt 1935, Travis & Post 1979).  
471 However, stable coexistence always occurs between facultative mutualists in models with  
472 saturating nullclines regardless of interaction strength. Conversely, in systems with at least one  
473 obligate partner, interactions must be sufficiently strong to overcome the negative intrinsic  
474 growth rate of the obligate partner for coexistence to be feasible (Bazykin *et al.* 1997). In this  
475 case, threshold effects can occur, not because of interaction strength but due to the low intrinsic  
476 growth rate of the partner. Overall, stronger interactions stabilize systems with threshold effects

by decreasing the threshold in population density that causes the system to collapse, which allows positive growth from lower densities.

In a network setting, weak, diffuse mutualistic interactions are considered stabilizing because their positive feedbacks are limited, and thus less likely to push the system away from equilibrium after a small perturbation (Bascompte *et al.* 2006, Allesina & Tang 2012). However, these studies have relied upon Lotka-Volterra-style models to represent mutualism. Theory that models mutualism with saturating benefits show that strong mutualistic interactions are stabilizing as expected from pairwise models (Holland *et al.* 2006, Okuyama & Holland 2008).

### *Effects of mutualism varies between low and high population density*

Empirical work has shown that the effects of mutualism vary with both recipient (Wolin & Lawlor 1984) and partner density (Holland 2015), and models show that this can lead to different ecological dynamics. When benefits are strongest at low recipient density, we can expect the robust dynamics of stable coexistence and threshold effects described previously (Fig. 2). When benefits are strongest at high recipient density, models predict unbounded growth unless limited by other intrinsic or extrinsic factors (compare Fig. 2C-D to Fig. 3I-K). When benefits are strongest at intermediate recipient density, we can expect saturating dynamics and emergent Allee effects (Fig. 4B). On the other hand, if benefits are strongest at low partner density and turn into net costs at high partner density, two outcomes are possible (Fig. 3, Fig. 4C): competitive or exploitative dynamics if the partner is at too high of an initial density, or potential oscillations to stable coexistence if the partners are well-balanced.

Early syntheses reported that mutualism with the strongest effects at high recipient density are less likely to be stable than those with the strongest effects at low recipient density (Addicott 1981, Wolin 1985). At that time, authors represented high-density effects of mutualism

as direct modifications to species' carrying capacity (Eqns 2, S9, S16; Wolin & Lawlor 1984). Authors now represent the effects of mutualism exclusively through changes in demographic rates (Holland 2015) unless explicitly representing habitat provisioning, e.g., corals or plants with domatia and their animal partners (Thompson *et al.* 2006). Mutualism may still have the strongest effects at high density (e.g., if benefits reduce negative density-dependence due to intraspecific competition or the Janzen-Connell effect), but this would be represented by modifying intraspecific limitation due to mutualism. Categorizing mutualisms by their relative magnitude of costs and benefits at low versus high density of recipients versus partners is still a profitable approach that could lead to a next-generation theoretical framework that organizes mutualism by their population dynamics. Additionally, separating out the specific demographic rates affected by mutualistic interactions (as in Thompson *et al.* 2006 and Hale *et al.* 2021) will likely clarify the differences and similarities between mutualisms. Even if the population dynamics of most models of mutualisms are qualitatively robust, the details of the low-density dynamics and the criteria for collapse can provide insight for system-specific mechanisms and patterns among them (Wu *et al.* 2019, Hale *et al.* 2021).

### *Costs of mutualism can cause damped and undamped oscillations*

Models that incorporate costs to the mutualistic interaction can exhibit the same qualitative dynamics described above. That is, they are stable when incorporating limiting factors to benefits and self-limitation, exhibit thresholds when at least one partner is obligate, and need strong interactions for obligate partners to persist. Additionally, these models can produce oscillations. Linear costs can result in damped oscillations when the equilibrium is a stable spiral (Fig. 3A-B; Neuhauser & Fargione 2004, Kang *et al.* 2011). Nonlinear costs can cause

undamped oscillations when the equilibrium is a stable center (Fig. 3G; Zhang 2003, Holland & DeAngelis 2010).

Undamped oscillations occur when overexploitation by the consumer causes an Allee effect in the resource, which does not necessarily lead to extinction (Fig. 3G). After depleting their resource population, the consumer population also declines, eventually allowing the resource to receive sufficient benefit compared to losses due to consumption. The system thus recovers, and coexistence is maintained in this region via a limit cycle (i.e., oscillations) around a stable center (left-most stable equilibrium, Fig. 3G). This outcome is not seen in simpler models without cost terms, which predict stable coexistence at a non-oscillatory node (Fig. 2), or with linear cost terms, which can predict damped-oscillations in a stable spiral (Fig. 3A-B).

Note that oscillation has been considered an important dynamic for mutualism models to reiterate, as justified by observations that mutualist populations can vary in space and time (Holland 2015). However, such variability need not necessarily be driven by the underlying population dynamics. Far simpler models of mutualism can produce oscillations when accounting for discrete time dynamics (e.g., Gilpin *et al.* 1982). This emphasizes that introducing explicit cost terms into mutualism should be adequately justified at the population level.

## Discussion

Theoretical study of mutualism has lagged behind the other two “pillars” of community ecology: competition and predator-prey interactions (Callaway 2007, Holland 2015). Early theory of mutualistic interactions was contemporaneous with early theory on predator-prey and competition interactions. After a gap of nearly 40 years, the destabilizing influence of mutualistic interactions in communities reignited theoretical attention. More recently, theory of mutualistic networks has made faster progress than that of pairwise mutualisms (Bascompte *et al.* 2003,

2006, Holland *et al.* 2006, Okuyama & Holland 2008, Thébault & Fontaine 2010, Valdovinos *et al.* 2013, 2016, 2018, Valdovinos 2019, Hale *et al.* 2020), and has also garnered more attention from broader community ecology (e.g., McCann & Gellner 2020).

We found that many historical models make similar qualitative predictions despite their different derivations, mechanisms, and inspiring systems. When feasible, coexistence is stable, and populations grow with bound. Mutualisms with at least one obligate partner exhibit thresholds, under which the low density of one partner destabilizes the system. If a species sustains nonlinear, population-level costs from mutualism, it may be overexploited to extinction by its partner. These patterns suggest that there exists a robust population dynamic theory of mutualism that can make general predictions. With this groundwork of theory laid, authors can now focus on how relaxing the assumptions of current models affects their predictions. For example, spatial and transmission models reiterate the threshold predictions of models that conform to the mean-field assumption (Ingvarsson & Lundberg 1995, Mohammed *et al.* 2018) as do models with explicit rewards dynamics compared to those that approximate steady-state (Revilla 2015, Wang 2019).

Future work should also understand how predictions from pairwise models scale to the network level. Threshold effects only occur when at least one partner is an obligate mutualist. Most species have multiple potential partners and thus are not truly “obligate” in the sense that only a specific pairwise interaction can allow positive population growth. Instead, most mutualists are likely to be facultative, engaging in diffuse interactions with many potential partners. However, it is likely that mortality exceeds reproduction in the absence of mutualistic interactions for many species. In this sense, species may be obligate mutualists even though they have multiple partners. Additionally, species are likely to have critical (cumulative) thresholds to

allow population growth. For example, Valdovinos and Marsland (2021) identify the quality of visits needed from pollinators for plants to persist. Below such threshold, the plant species and the animals depending on those plants go extinct. Understanding how destabilizing thresholds may emerge or be ameliorated due to obligate mutualists in a network setting is an important goal for future work. Moreover, emphasis on consumer-resource approaches with a common “currency” of energy or biomass flows (Holland 2015) make mutualisms amenable to integration into interspecific network models such as food webs (e.g., Hale *et al.* 2020). Such integration can illuminate how context mediates interaction outcomes between potential mutualists, for example by shifting interactions into overexploitation or competition regimes. Indeed, understanding the structure and dynamics of these ‘multiplex’ ecological networks that include multiple types of interactions has been identified as a primary goal in ecology (Kéfi *et al.* 2012).

Future work should interrogate the assumptions and predictions of these models with empirical work. A main assumption is that mutualisms have population-level impacts. However, most empirical studies quantify the benefits and costs of mutualisms at the individual level in terms of fitness or even by using a single proxy for fitness (Bronstein 2001a, Ford *et al.* 2015). Those effects do not necessarily imply population- and community-level impacts of mutualism (Williamson 1972, Flatt & Weisser 2000, Palmer *et al.* 2010, Ford *et al.* 2015). Therefore, empirical work is of foremost importance to evaluate whether mutualisms affect the population dynamics of mutualistic partners. Among the predictions of these models (stable coexistence, threshold effects, overexploitation), threshold effects have received the most attention (Latty & Dakos 2019), but more empirical work is still needed. Wotton and Kelly (2011) and Kang *et al.* (2011) observed threshold effects directly in frugivory systems and in ant-fungal gardens, respectively, although the authors did not identify their results as such. Hale *et al.* (2021) showed

that threshold effects in obligate plants may be swamped out by Allee effects, which suggests that targeted experiments to explore population trajectories should consider the criteria for observing different dynamics (Fig. 4).

One difficulty of empirical applications is that an out-of-the-box consumer-resource approach following Holland and DeAngelis' (2010) framework can be logistically overwhelming. Nonlinear cost and benefit functions generate so many dynamics that they are nearly intractable analytically (but see numerical toolkit by Wu *et al.* 2019). Moreover, with up to four separate functional responses to parameterize, this framework requires an extremely high number of parameters to estimate empirically. This level of detail may be necessary to describe some two-species mutualism but is likely not general. Simplifications like approximating costs and benefits as proportional to consumers' foraging rate (Soberón & Martinez 1981, Revilla 2015, Hale *et al.* 2021) can facilitate integration between theoretical and empirical approaches. Additionally, costs that scale with rewards construction can be approximated as fixed reductions to benefit, and thus accounted for in the measured parameters (Revilla 2015, Hale *et al.* 2021). Systems with these complementary saturating benefits and fixed costs are likely to display much more limited dynamics than those shown in Fig. 3C-G. For example, Kang *et al.* (2011) and Martignoni *et al.* (2020) adapted Holland and DeAngelis' approach to specific empirical systems, leading to models which predict the threshold and stable coexistence dynamics of simpler saturating benefit models (Fig. 3H-J).



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## Legends

**Fig. 1. Characteristic dynamics for linear benefit models.** In early models of mutualism, benefits were represented by a constant coefficient (interactions strength) multiplying a linear function of partner density. Benefits affected per-capita growth rate (low-density effect, **A**), equilibrium density (high-density effect, **B**), or both (**C-F**). High- and both low- and high-density effects (**B-F**) yield the same nullclines (curves of the zero growth), but species achieve equilibrium density faster when mutualism affects both their equilibrium density and their per-capita growth rate. When mutualists are facultative partners ( $N_i = K_i > 0$  when  $N_j = 0$ ), they can display unbounded growth or stable coexistence depending on whether benefits were strong (**C**) or weak (**D**). When mutualists are obligate partners ( $N_i = K_i \leq 0$  when  $N_j = 0$ ), they observed stable coexistence or extinctions when mutualists were strong (**E**) or weak (**F**). When mutualists are a facultative-obligate pair, they display any of the previous four results depending on relative interaction strength and obligacy (e.g., **B**, see Vandermeer & Boucher for full results). Panels show: (**A**) Addicott 1981, (**B**) Whittaker 1978, (**C-F**) Gause & Witt 1935, Vandermeer & Boucher 1978. Benefit strength (weak or strong) is relative to intraspecific limitation. Arrows are vectors showing the ‘flow’ of the system: arrow angle shows the direction of changes in density of  $N_1$  (x-direction) and  $N_2$  (y-direction) and arrow color shows the magnitudes of change in that direction (lighter colors are stronger changes). Nullclines are curves of zero change of density for one partner. Equilibria (colored or hollow dots) occur when both partners have zero change in density. Equilibria are locally stable (black dots) or unstable (red dots) if the system is attracted or repelled, respectively, the equilibrium after a small perturbation. Equilibria are half-stable “saddles” (hollow dots) if the system is attracted in some dimensions by repelled in others.

**Fig. 2. Characteristic dynamics for saturating benefit models.** Density-dependent benefit functions stabilize linear benefit models (Fig. 1). Benefits may saturate (decrease in strength) with increasing recipient density (“intraspecific density-dependence,” **A-B**), increasing partner density (“interspecific density-dependence,” **E-J**), or both (**K**), resulting in stable coexistence. Benefits may also increase in strength with increasing recipient density (another form of intraspecific density-dependence), causing unbounded growth in the absence of other limitations (**C-D**). Models where at least one partner exhibits saturating benefits and intraspecific limitation exhibit the same qualitative dynamics (**A-B, E-K**): feasible systems display stable coexistence at densities higher than either partner could achieve alone (off-axes black point), and potential or guaranteed threshold effects when one or both partners are obligate mutualists. Under a certain threshold (red dashed line), one population is at too low density to support its partner, collapsing the system (**F, H, J, K**). This threshold causes extinction of obligate partners, even if initially highly abundant (e.g., follow lighter colored trajectories in panel **F**). These dynamics of coexistence and threshold effects are robust across models of mutualism with saturating benefits, regardless of the mechanism by which benefit saturates. Panels show models ordered chronologically: (**A**) Whittaker 1975, (**B-D**) Wolin & Lawlor 1985, (**E-F**) Wright 1989, (**G-H**) Graves *et al.* 2006, (**I-J**) Thompson *et al.* 2006, (**K**) Fishman & Hadany 2010. Models are also ordered by increasing mechanistic detail, from arbitrary limiting factors applied to Lotka-Volterra models (**A**) to a population-level approximation of benefit functions from an individual-based model (**K**). These models represent diverse inspiring systems, including host-symbiont (**A**), pollination (**E-F, K**), lichens (**G-H**), and protection mutualism (**I-J**).

**Fig. 3. Characteristic dynamics for shifting net-effects and consumer-resource models.**

Models that investigated shifts in net effects as a balance of costs and benefits led to a synthesis of mutualism into a consumer-resource framework. Models with saturating benefit functions and linear costs (**A-B**) tend to display stable coexistence (**A**) and threshold effects (**B**) like earlier models (Fig. 2). Stable coexistence is “mutualistic” if the nullclines intersect such that both species achieve higher density than they would alone, or if increasing the density of one species from equilibrium permit growth of its partner. Otherwise, the interaction is “parasitic” (in this case, if the linear nullcline intersected above the vertex of the curved nullcline). Linear costs can make the coexistence equilibrium a stable spiral, with damped oscillations towards equilibrium (**B, D, E, G, H**). Models with unimodal benefit response that allow negative effects (net costs) at high density (**C-E**) or that include both separately saturating costs and benefits (**F-G**) display more complex dynamics. Depending on its parameterization, the mutualism-competition model by Zhang (2003) displays competitive exclusion (**C**), mutualistic stable coexistence (**D**), or competitive dominance (**E**), with dominant species dependent on initial densities (i.e., system initialized to the left or right of the separatrix). The consumer-resource model by Holland & DeAngelis (2010) also displays a range of dynamics depending on parameterization (**E-F**), including multiple stable coexistence equilibria (**F**). Mutualistic coexistence occurs when the ratio of consumers to their resources is not above a certain threshold (i.e., to the left of the left separatrix, or below the bottom separatrix). Otherwise, consumers overexploit their resources (causing more costs than provided benefits), leading to system collapse. Panels show the following models: (**A-B**) Neuhauser & Fargione 2004 (plant-mycorrhizae), (**C-E**) Zhang 2003 (competitor-mutualists), (**F-G**) Holland & DeAngelis 2010 (bidirectional consumer-resource

mutualism, e.g., corals), (**H**) Kang *et al.* 2011 (ant-fungal garden), (**I-J**) Martignoni *et al.* 2020 (plant-mycorrhizae), (**K**) Hale *et al.* 2021 (plant-seed disperser).

**Fig. 4. Distinguishing characteristic dynamics.** N1 (x-axis) is obligate mutualist and N2 (y-axis) is facultative in all panels. (**A**) Threshold effects: N1 goes extinct when the density of N2 is below certain threshold (separatrix), or the system achieves stable coexistence when N2 is above such threshold, where both species achieve higher densities than each would attain alone. (**B**) Overexploitation dynamics: the system collapses above a threshold in the ratio of consumer (N2) to resource (N1) species density. At low density, both partners will grow due to benefits from mutualism until they reach stable coexistence at higher density than either species could achieve alone. Above a threshold of N2 density (separatrix), both populations will grow but N2 will increase to such an extent that it exerts more costs than benefits it provides (exploitation). N1 will begin to decline at low density while N2 continues to grow, eventually leading to both going extinct. At even higher initial densities of N2, N2 will immediately overexploit N1 and both species will go extinct, without even acquiring enough benefits to allow its own population to grow. (**C**) Allee effects: N1 will go extinct if its density is under certain threshold (separatrix) because it becomes too rare to receive benefits from the mutualistic interaction. The system tends towards stable coexistence at higher density than either partner could achieve alone when N1 is above such threshold of its own density. Note that overexploitation (**B**) by the high-density consumer (N2) induces an Allee effect in the resource species (N1) where lower resource density causes lower benefits from the interaction. Example systems: (**A**) Graves *et al.* 2006, lichens; (**B**) Holland & DeAngelis 2010, unidirectional consumer resource mutualism (e.g., seed dispersal); (**C**) Hale *et al.* 2021, pollination.

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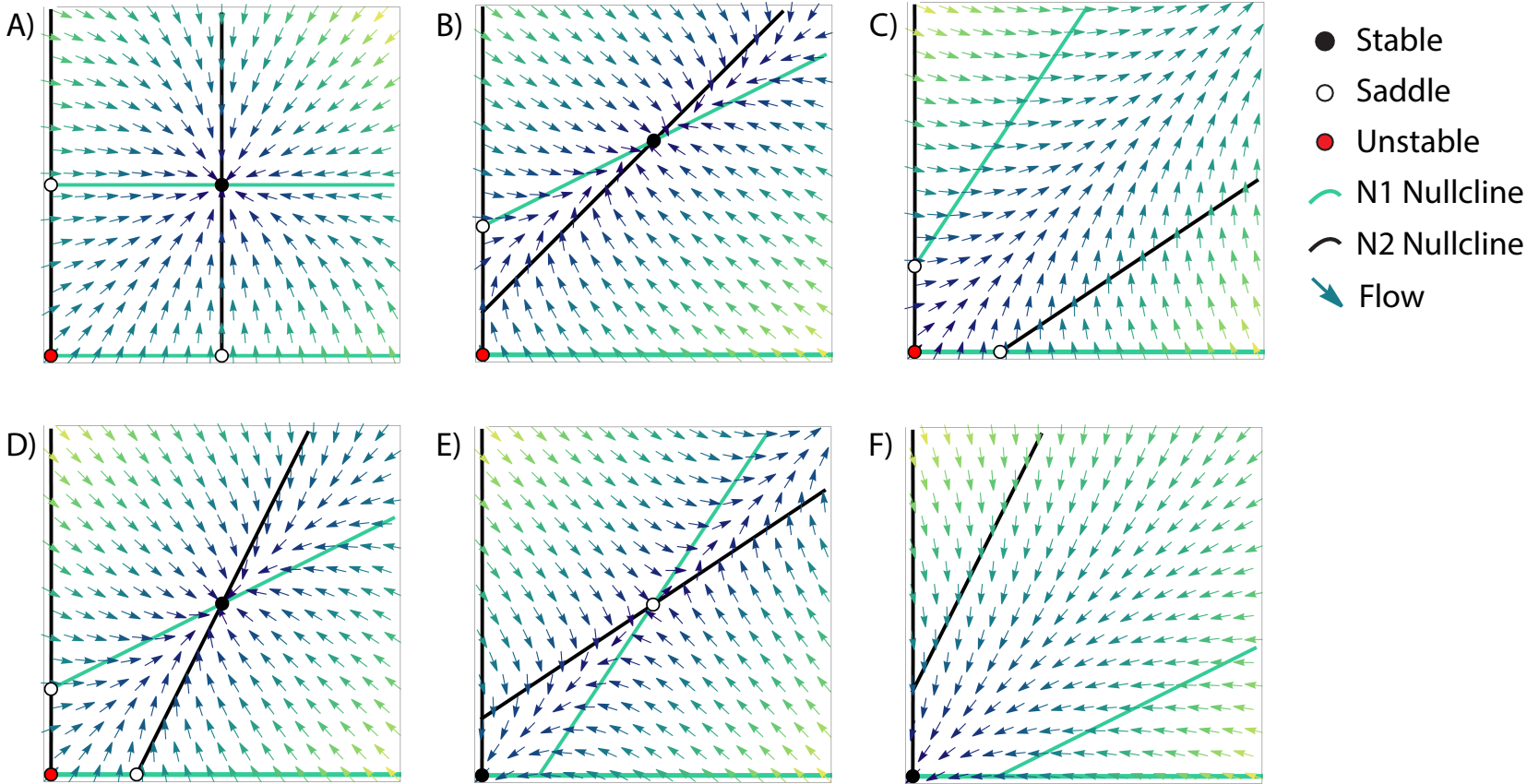
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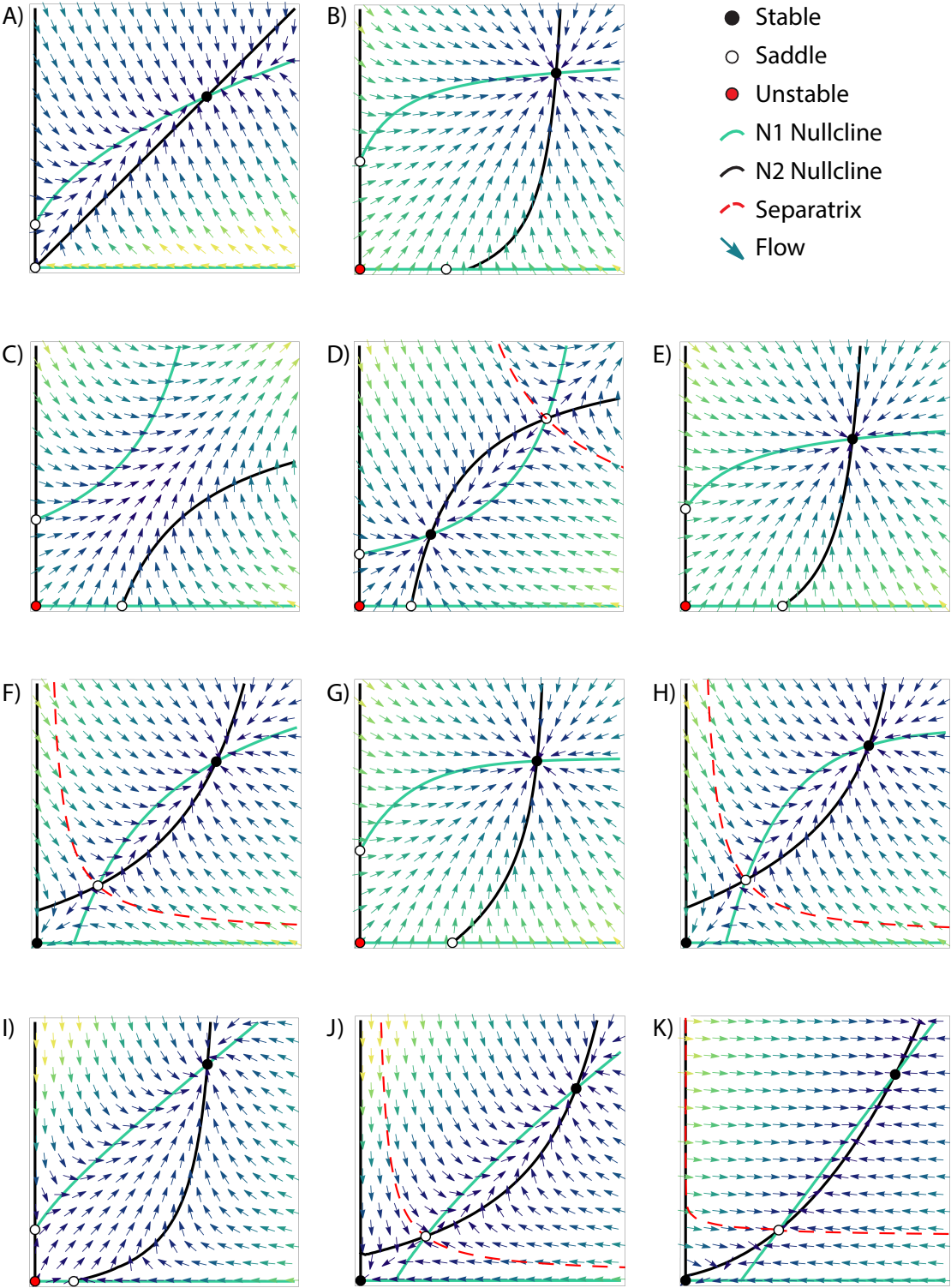
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Figures

Fig. 1. Characteristic dynamics for linear benefit models.



919 **Fig. 2. Characteristic dynamics for saturating benefit models.**

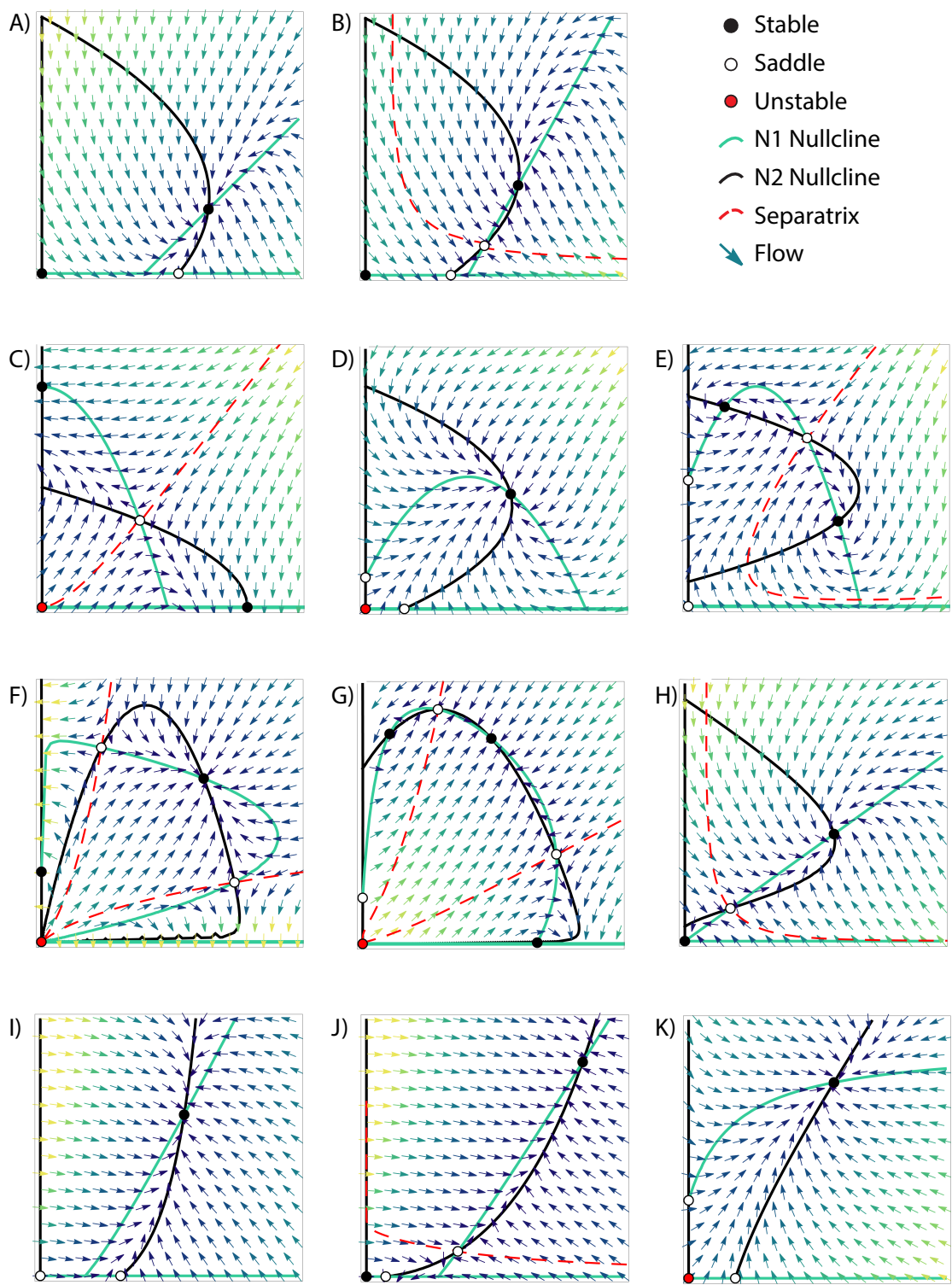


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922 **Fig. 3. Characteristic dynamics for shifting net-effects and consumer-resource models.**

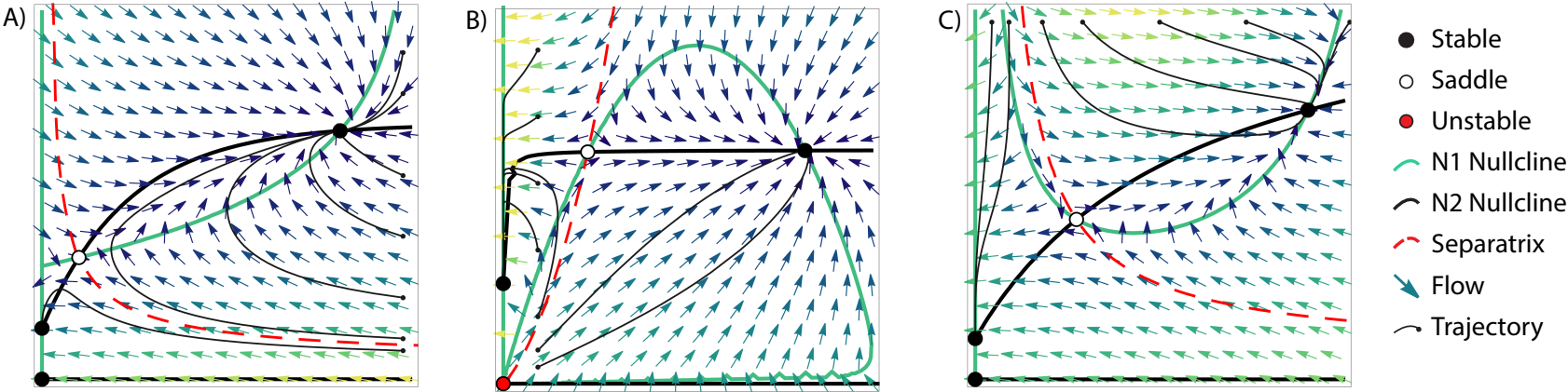


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925 **Fig. 4. Distinguishing characteristic dynamics.**

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928 **Table 1. The historical development of theory of mutualism.**

	<b>Linear benefits</b>	<b>Saturating benefits (<i>intraspecific</i>)</b>	<b>Saturating benefits (<i>interspecific</i>)</b>	<b>Cost-benefit models &amp; shifting net effects</b>	<b>Consumer-resource approach</b>
<b>Beginning</b>	Gause & Witt (1935) proposed the first mutualism model as a modification of the Lotka-Volterra equations.	Whittaker (1975) proposed that benefits to a host population from a symbiont should saturate per host individual due to extrinsic factors.	Wright (1989) proposed that benefits should saturate with interspecific density, due to constraints on handling time.	Hernandez (1998) proposed that benefits increase at low partner density, but interaction becomes negative at high partner density.	Holland & DeAngelis (2010) proposed that resource supply and consumption processes directly affect per-capita growth rate.
<b>Mechanisms included</b>	Benefit increases per-capita growth rate (low-density effect), equilibrium density (high-density effect), or both.	Benefits decrease as: Resources or space become limiting*, Substrates to receive or attract benefits become limiting, Competition for benefits increases. * “extrinsic” factors; all other listed limitations are “intrinsic” to the mutualism	Rate of benefit accrual decreases as (effective) partner density becomes limiting, or due to satiation, search time, or handling time. Benefits may also be subject to intraspecific limitations.	Partners have nonlinear effects, with positive effects (net benefits) at low partner density and negative effects (net costs) at high partner density. Benefits accrue due to exploitation facilitation at low density. Costs accrue due to exploitation or competition at high density.	Benefits accrue due to consumption of resources (or services) supplied by a partner. Costs accrue by supplying resources to a partner or having resources consumed.
<b>Characteristic assumptions</b>	Benefit is a linear function of partner density.	Benefit increases per-capita growth rate and equilibrium density, but saturates with increasing recipient density. At least one partner experiences additional self-limitation.	Benefit increases per-capita growth rate and equilibrium density, but saturates with increasing partner density. At least one partner experiences additional self-limitation	Net effects are represented directly as a non-monotonic interspecific function or emerge from the balance between interspecific benefit and cost functions	Consumption is an interspecific process. Services are approximated as function of partner density or consumption rate. Costs accrue in demographic or foraging parameters (“fixed costs”), or are functions

					of partner consumption rate (“variable costs”)
<b>Predictions</b>	<p>Unbounded growth between facultative partners with strong interactions.</p> <p>Stable coexistence between facultative partners with weak interactions.</p> <p>Extinction of obligate partners below a certain density threshold or unbounded growth above such threshold with strong interactions.</p> <p>Extinction of obligate partners with weak interactions.</p>	<p>Stable coexistence in feasible interactions, regardless of interaction strength or obligacy.</p> <p>Threshold between extinction of obligate partners and stable coexistence when at least one partner is obligate.</p> <p>Coexistence is non-oscillatory (stable node).</p>	Same predictions as in intraspecific saturating models.	<p>Diverse dynamics, depending on the model and its parameterization:</p> <p>Predictions of saturating models, but coexistence may be oscillatory (stable spiral)</p> <p>Mutualistic coexistence, competitive coexistence, or competitive exclusion</p> <p>Mutualistic coexistence, parasitic coexistence, or extinctions.</p>	<p>Fixed costs: same predictions as in saturating models.</p> <p>Variable, linear costs: same predictions as saturating models, but coexistence may be oscillatory.</p> <p>Variable, nonlinear costs: mutualistic coexistence or overexploitation by consumers leading to collapse; coexistence may be oscillatory.</p>
<b>Citations</b>	Gause & Witt 1935, Whittaker 1974, Vandermeer & Boucher 1978, Goh 1979, Addicott 1981.	Whittaker 1975, May 1976, Soberón & Martinez del Rio 1981, Dean 1983, Wolin & Lawlor 1984.	Wells 1983, Pierce & Young 1986, Wright 1989, Graves <i>et al.</i> 2006, Thompson <i>et al.</i> 2006, Fishman & Hadany 2010, Johnson & Amarasekare 2013, García-Algarra <i>et al.</i> 2014.	Hernandez 1998, Holland <i>et al.</i> 2002, Neuhauser & Fargione 2004, Wu <i>et al.</i> 2019.	Holland & DeAngelis 2010, Kang <i>et al.</i> 2011, Revilla 2015, Martignoni <i>et al.</i> 2020, Hale <i>et al.</i> 2021.

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931 **Table 2. Selected models of pairwise mutualism.** A full list of models cited in the main text is  
932 included in the supplementary information (Table S1). Equations largely follow the notation  
933 from the original citations. All parameters are positive ( $> 0$ ) unless otherwise specified. Models  
934 with unique mathematical forms are given unique equation numbers. We encourage the readers  
935 to refer to the original references for the model derivations and interpretation of parameters.  
936 Notes include inspiring system and obligacy, if specified by authors.

Reference	Eqn	Models for Pairwise Mutualism ( $i = 1, 2$ )	Notes
Gause & Witt 1935	1	$\frac{dN_i}{dt} = r_i N_i \left( \frac{K_i + \alpha_{ij} N_j - N_i}{K_i} \right)$	Facultative only
Whittaker 1975	2 1	$\begin{cases} \frac{dN_1}{dt} = r_1 N_1 \left( \frac{K_1 + \alpha_{12} N_2 - N_1}{K_1 + \alpha_{12} N_2} \right) \\ \frac{dN_2}{dt} = r_2 N_2 \left( \frac{K_2 + \alpha_{21} N_1 - N_2}{K_2} \right) \end{cases}$	Symbiont ( $N_1$ )-Host ( $N_2$ ) Obligate $N_1$ when $K_1 = 0$ Parasitism when $\alpha_{21} < 0$
	2 3	$\begin{cases} \frac{dN_1}{dt} = r_1 N_1 \left( \frac{\alpha_{12} N_2 - N_1}{\alpha_{12} N_2} \right) \\ \frac{dN_2}{dt} = \frac{r_2 N_2}{K_2} \left( K_2 + \frac{a D N_1}{D + N_2} - N_2 \right) \end{cases}$	Symbiont ( $N_1$ )-Host ( $N_2$ ) Obligate $N_1$
Vandermeer & Boucher 1978	1	$\frac{dN_i}{dt} = N_i (r_i + \alpha_{ij} N_j - \alpha_{ii} N_i)$	Legume ( $N_1$ )- <i>Rhizobium</i> ( $N_2$ ) Obligate when $K_i = r_i / \alpha_{ii} \leq 0$
Addicott 1981	4	$\frac{dN_i}{dt} = r_i N_i \left( \frac{K_i - N_i}{K_i} \right) \left( 1 + \frac{\alpha_{ij} N_j}{K_i} \right)$	Aphid ( $N_1$ )-Ant ( $N_2$ ) Facultative only See Table S1
Wolin & Lawlor 1984	5	$\frac{dN_i}{dt} = N_i \left( r_i - \frac{b N_i}{1 + m N_j} - d N_i \right)$	Facultative only Reduces intra-specific limitation in birth ( $b$ ) to at most 0 See Table S1
	6	$\frac{dN_i}{dt} = N_i (r_i - (b - m N_j + d) N_i)$	Reduces $b$ without limit
Wright 1989	7	$\frac{dN_i}{dt} = N_i \left( r_i - c_i N_i + b_{ij} \frac{a_{ij} N_j}{1 + a_{ij} h_{ij} N_j} \right)$	Pollinators & other forager mutualists See Table S1
Zhang 2003	8	$\frac{dN_i}{dt} = R_i N_i (c_i - N_i - a_i (N_j - b_i)^2)$	Interactions between species at the same trophic level $-\infty < b_i < \infty$

Neuhauser & Fargione 2004	9 1	$\begin{cases} \frac{dN_1}{dt} = r_1 N_1 \left( \frac{K_1 + \gamma_{12} N_2 - N_1}{K_1 + \gamma_{12} N_2} - a N_2 \right) \\ \frac{dN_2}{dt} = r_2 N_2 \left( \frac{K_2 + \alpha_{21} N_1 - N_2}{K_2} \right) \end{cases}$	Plant ( $N_1$ )-Mycorrhizae ( $N_2$ ) Facultative only
Graves <i>et al.</i> 2006	10	$\frac{dN_i}{dt} = N_i (r_{i0} + (r_{i1} - r_{i0})(1 - e^{-k_i N_j}) - a_i N_i)$	Lichens Obligate when $r_{i0} < 0, r_{i1} + r_{i0} > 0$ See Table S1
Thompson <i>et al.</i> 2006	11 12	$\begin{cases} \frac{dN_1}{dt} = (\rho_1 b_1 N_1 + I_1) \left( 1 - \frac{N_1}{S_1} \right) - \left( d_{1min} + \frac{d_{1max} - d_{1min}}{1 + c_1 N_2} \right) N_1 \\ \frac{dN_2}{dt} = (\rho_2 b_2 N_2 + I_2) \left( 1 - \frac{N_2}{S_2 + N_1} \right) - \left( d_{1min} + \frac{d_{2max} - d_{2min}}{1 + c_2 N_1} \right) N_2 \end{cases}$	Hermit crabs ( $N_1$ )-Anemones ( $N_2$ ) Closed system when $I_i = 0, \rho_i = 1$ Obligate when $\rho_i b_i < d_{imax}$ See Table S1
Holland & DeAngelis 2010	13	$\frac{dN_i}{dt} = N_i \left( r_i + c_i \left( \frac{a_{ij} N_j}{h_j + N_j} \right) - q_i \left( \frac{\beta_{ij} N_j}{e_i + N_i} \right) - s_i N_i \right)$	Bidirectional Consumer-Resource e.g., Plant ( $N_1$ )-Mycorrhizae ( $N_2$ ) Obligate when $r_i = 0$
	13 7	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( r_1 + c_1 \left( \frac{a_{12} N_2}{h_2 + N_2} \right) - q_1 \left( \frac{\beta_{12} N_2}{e_1 + N_1} \right) - s_1 N_1 \right) \\ \frac{dN_2}{dt} = N_2 \left( r_2 + c_2 \left( \frac{a_{21} N_1}{h_1 + N_1} \right) - s_2 N_2 \right) \end{cases}$	Unidirectional e.g., Plant ( $N_1$ )-Pollinator ( $N_2$ )
Fishman & Hadany 2010	14 15	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( \frac{\eta \alpha N_2}{1 + \alpha N_1 + \alpha \beta N_2} - b - c N_1 \right) \\ \frac{dN_2}{dt} = N_2 \left( \frac{\mu \alpha N_1}{1 + \alpha N_1 + \alpha \beta N_2} - d \right) \end{cases}$	Plant ( $N_1$ )-Pollinator ( $N_2$ ) Obligate only
Kang <i>et al.</i> 2011	16 1	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( r_f \left( \frac{a N_2^2}{b + a N_2^2} \right) - r_c N_2 - d_1 N_1 \right) \\ \frac{dN_2}{dt} = N_2 (r_a N_1 - d_2 N_2) \end{cases}$	Fungal garden ( $N_1$ )-Leaf cutter ant ( $N_2$ ) Obligate only
Martignoni <i>et al.</i> 2020	17 18	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( r_p + \frac{q_{hp} \alpha N_2}{d + N_1} - q_{cp} \beta N_2 - \mu_p N_1 \right) \\ \frac{dN_2}{dt} = N_2 \left( q_{cm} \beta N_1 - \frac{q_{hm} \alpha N_1}{d + N_1} - \mu_m N_2 \right) \end{cases}$	Plant ( $N_1$ )-Mycorrhizae ( $N_2$ ) Obligate $N_2$
Hale <i>et al.</i> 2021	19 7	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( \left( b_1 + \beta \frac{a N_2 N_1}{1 + a h N_1} \right) g (1 - s_1 N_1) - d_1 \right) \\ \frac{dN_2}{dt} = N_2 \left( b_2 + \varepsilon \frac{a N_1}{1 + a h N_1} - s_2 N_2 - d_2 \right) \end{cases}$	Plant ( $N_1$ )-Pollinator ( $N_2$ ) Obligate $N_1$ when $b_1 g - d_1 \leq 0$ ; obligate $N_2$ when $b_2 - d_2 \leq 0$
	20 7	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( b_1 g \left( 1 - \left( s_1 - \sigma \frac{a N_2}{1 + a h N_1} \right) N_1 \right) - d_1 \right) \\ \frac{dN_2}{dt} = N_2 \left( b_2 + \varepsilon \frac{a N_1}{1 + a h N_1} - s_2 N_2 - d_2 \right) \end{cases}$	Facultative $N_1$ only

## Supplementary Information

**Table S1. Models of pairwise mutualism.** Equations largely follow the notation from the original citations. All parameters are positive ( $> 0$ ) unless otherwise specified. Models with unique mathematical forms are given unique equation numbers, starting chronologically (compared to the selected models from main text). We encourage the readers to refer to the original references for the model derivations and interpretation of parameters. Notes include inspiring system and obligacy, if specified by authors.

Reference	Eq n	Models for Pairwise Mutualism ( $i = 1, 2$ )	Notes (inspiring system, obligacy, etc.)
Gause & Witt 1935	S1	$\frac{dN_i}{dt} = r_i N_i \left( \frac{K_i + \alpha_{ij} N_j - N_i}{K_i} \right)$	Facultative only
Whittaker 1975	S2	$\begin{cases} \frac{dN_1}{dt} = r_1 N_1 \left( \frac{K_1 + \alpha_{12} N_2 - N_1}{K_1 + \alpha_{12} N_2} \right) \\ \frac{dN_2}{dt} = r_2 N_2 \left( \frac{K_2 + \alpha_{21} N_1 - N_2}{K_2} \right) \end{cases}$	Symbiont ( $N_1$ )-Host ( $N_2$ ) Obligate $N_1$ when $K_1 = 0$ Parasitism when $\alpha_{21} < 0$
	S1		
	S2	$\begin{cases} \frac{dN_1}{dt} = r_1 N_1 \left( \frac{\alpha_{12} N_2 - N_1}{\alpha_{12} N_2} \right) \\ \frac{dN_2}{dt} = \frac{r_2 N_2}{K_2} \left( K_2 + \frac{a d N_1}{D + N_2} - N_2 \right) \end{cases}$	Obligate Symbiont ( $N_1$ )-Host ( $N_2$ ) Arbitrary external factors limit benefit to $N_2$
	S3		
May 1976	S4	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( \frac{I N_2}{C D + C N_1 + N_1 N_2} - d_1 \right) \\ \frac{dN_2}{dt} = r_2 N_2 \left( \frac{\alpha_{21} N_1 - N_2}{\alpha_{21} N_1} \right) \end{cases}$	Plant ( $N_1$ )-Pollinator ( $N_2$ ) and others
	S2		
Vandermeer & Boucher 1978	S1	$\frac{dN_i}{dt} = N_i (r_i + \alpha_{ij} N_j - \alpha_{ii} N_i)$	Legume ( $N_1$ )- <i>Rhizobium</i> ( $N_2$ ) Obligate when $K_i = r_i / \alpha_{ii} \leq 0$
Addicott 1981	S5	$\frac{dN_i}{dt} = r_i \left( \frac{K_i - N_i}{K_i} \right) \left( 1 + \frac{\alpha_{ij} N_j}{K_i} \right)$	Aphid ( $N_1$ )-Ant ( $N_2$ ) Facultative only
	S6	$\frac{dN_i}{dt} = r_i N_i \left( \frac{K_i - N_i}{K_i} \right) \left( 1 + \frac{\alpha_{ij} N_j}{K_i} \right)$	*Reference reports Eqn. 5. Figures suggest Eqn. 6 & subsequent authors use Eqn. 6
Soberón & Martinez del Rio 1981	S7	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( \frac{k_1 \sigma \mu N_2}{1 + \sigma \phi \mu^2 N_1} - \gamma \right) \\ \frac{dN_2}{dt} = N_2 \left( \epsilon (K_2 - N_2) + \frac{k_2 \sigma \mu^2 N_1}{1 + \sigma \phi \mu^2 N_1} \right) \end{cases}$	Plant ( $N_1$ )-Pollinator ( $N_2$ ) Obligate $N_1$ ; obligate $N_2$ when $K_2 = 0$
	S8		
Dean 1983	S9	$\frac{dN_i}{dt} = r_i N_i \left( \frac{k_i - N_i}{k_i} \right)$ $k_i = K_{i \max} (1 - e^{-(\alpha_i N_j + c_i) / K_{i \max}})$	Unintended behaviors; updated by Graves <i>et al.</i> 2006
Wells 1983	S10	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( \frac{b N_2}{a N_1 + N_2 + c} - d f N_1 - d \right) \\ \frac{dN_2}{dt} = N_2 \left( \frac{m N_1}{r N_2 + N_1 + h} - g \right) \end{cases}$	Plant ( $N_1$ )-Pollinator ( $N_2$ ) Obligate only
	S11		
Wolin & Lawlor 1984	S12	$\frac{dN_i}{dt} = N_i \left( r_i - \frac{b N_i}{1 + m N_j} - d N_i \right)$	Multiple models (including S2, S6) where benefits are a fn. of intra-specific limitation in birth ( $b$ ) & death ( $d$ ) processes Facultative only Reduces $b$ to at most 0

	S13	$\frac{dN_i}{dt} = N_i(r_i - (b - mN_j + d)N_i)$	Reduces $b$ without limit
	S14	$\frac{dN_i}{dt} = N_i\left(r_i\left(1 - \frac{N_i}{K}\right) + mN_j e^{-\alpha N_i}\right)$	Benefits decrease exponentially
Pierce & Young 1986	S15 S16	$\begin{cases} \frac{dN_1}{dt} = N_1\left(r_1(N_2) - \frac{N_1}{K_1}\right) \\ \frac{dN_2}{dt} = r_2 N_2\left(1 - \frac{N_2}{K_2(N_1)}\right) \end{cases}$	Lycaenid ( $N_1$ )-Ant ( $N_2$ ) $r_1(N_2)$ is 1's growth rate as a fn. of $N_2$ ; $K_2(N_1)$ is 2's equilibrium density of 2 as a fn. of $N_1$ . Parasitism when $K_2(N_1)$ is decreasing
Wright 1989	S17	$\frac{dN_i}{dt} = N_i\left(r_i(1 - c_i N_i) + b_{ij} \frac{a_{ij} N_j}{1 + a_{ij} h_{ij} N_j}\right)$	Pollinators & other forager mutualists
	S8	$\frac{dN_i}{dt} = N_i\left(r_i - c_i N_i + b_{ij} \frac{a_{ij} N_j}{1 + a_{ij} h_{ij} N_j}\right)$	*Reference reports Eqn 17. Figures suggest Eqn 8 & subsequent authors use Eqn 8 Obligate when $r_i < 0$
Hernandez 1998	S18	$\frac{dN_i}{dt} = r_i N_i\left(1 - \frac{N_i}{K_i} + \left(\frac{b_i N_j - c_i N_j^2}{1 + d_i N_j^2}\right) \frac{N_j}{K_i}\right)$	Facultative Parasitism at high $N_j$
	S19	$\frac{dN_i}{dt} = r_i N_i\left(-1 + \left(\frac{b_i N_j - c_i N_j^2}{1 + d_i N_j^2}\right) \frac{N_j}{K_i}\right)$	Obligate Parasitism at high $N_j$
Holland <i>et al.</i> 2002	S20 S21	$\begin{cases} \frac{dN_1}{dt} = N_1\left((1-a)\alpha F\left(1 - e^{\left(\frac{-\gamma_1 N_2}{FN_1}\right)}\right)\left(e^{\left(\frac{-\gamma_2 N_2}{FN_1}\right)}\right) - d_1 - gN_1\right) \\ \frac{dN_2}{dt} = (1-a)\alpha F\left(1 - e^{\left(\frac{-\gamma_1 N_2}{FN_1}\right)}\right)\left(e^{\left(\frac{-\gamma_2 N_2}{FN_1}\right)}\right) - d_2 N_2 \end{cases}$	Obligate Senita Cactus ( $N_1$ ) – Moth ( $N_2$ ) Detailed application of more general theory
Zhang 2003	S22	$\frac{dN_i}{dt} = R_i N_i (c_i - N_i - a_i (N_j - b_i)^2)$	Interactions between species at the same trophic level Competition at high $N_j$ $\infty < b_i < \infty$
Neuhauser & Fargione 2004	S23 S1	$\begin{cases} \frac{dN_1}{dt} = r_1 N_1\left(1 - \frac{N_1}{K_1 + \gamma_{12} N_2} - aN_2\right) \\ \frac{dN_2}{dt} = r_2 N_2\left(\frac{K_2 + \alpha_{21} N_1 - N_2}{K_2}\right) \end{cases}$	Plant ( $N_1$ )-Mycorrhizae ( $N_2$ ) Facultative only
Graves <i>et al.</i> 2006	S9	$\frac{dN_i}{dt} = N_i(r_{i0} + (r_{i1} - r_{i0})(1 - e^{-k_i N_j}) - a_i N_i)$	Lichens and other N-fixing symbioses Updates Dean's (1983) model so that mutualism affects per-capita growth rate instead of equilb. density directly. Obligate when $r_{i0} < 0, r_{i1} + r_{i0} > 0$
Thompson <i>et al.</i> 2006	S24	$\frac{dN_i}{dt} = \left(\rho_i \left(b_i N_i + \frac{\alpha_i N_j}{\beta_i + N_j} N_i\right) + I_i\right) \left(1 - \frac{N_i}{S_i}\right) - d_{i_{max}} N_i$	Set of models with different combinations of benefit. Closed system when $I_i = 0$ , $\rho_i = 1$ . Obligate when $\rho_i b_i < d_{i_{max}}$ Benefit: increases birth
	S25	$\frac{dN_i}{dt} = (\rho_i b_i N_i + I_i) \left(1 - \frac{N_i}{S_i}\right) - \left(d_{i_{min}} + \frac{d_{i_{diff}}}{1 + c_i N_j}\right) N_i$	Decreases death
	S26	$\frac{dN_i}{dt} = (\rho_i b_i N_i + I_i) \left(1 - \frac{N_i}{S_i + N_j}\right) - d_{i_{max}} N_i$	Increases carrying capacity



Holland & DeAngelis 2010	S27	$\frac{dN_i}{dt} = N_i \left( r_i + c_i \left( \frac{a_{ij}N_j}{h_j + N_j} \right) - q_i \left( \frac{\beta_{ij}N_j}{e_i + N_i} \right) - s_i N_i \right)$	Bidirectional Consumer - Resource e.g., Plant ( $N_1$ )-Mycorrhizae ( $N_2$ )
	S27 S8	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( r_1 + c_1 \left( \frac{a_{12}N_2}{h_2 + N_2} \right) - q_1 \left( \frac{\beta_{12}N_2}{e_1 + N_1} \right) - s_1 N_1 \right) \\ \frac{dN_2}{dt} = N_2 \left( r_2 + c_2 \left( \frac{a_{21}N_1}{h_1 + N_1} \right) - s_2 N_2 \right) \end{cases}$	Unidirectional e.g., Plant ( $N_1$ )-Pollinator ( $N_2$ ) Obligate when $r_i = 0$
Fishman & Hadany 2010	S10 S11	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( \frac{\eta\alpha N_2}{1 + \alpha N_1 + \alpha\beta N_2} - b - cN_1 \right) \\ \frac{dN_2}{dt} = N_2 \left( \frac{\mu\alpha N_1}{1 + \alpha N_1 + \alpha\beta N_2} - d \right) \end{cases}$	Plant ( $N_1$ )-Pollinator ( $N_2$ ) Obligate only Approx. from individual-based model
Kang <i>et al.</i> 2011	S28 S1	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( r_f \left( \frac{aN_2^2}{b + aN_2^2} \right) - r_c N_2 - d_1 N_1 \right) \\ \frac{dN_2}{dt} = N_2 (r_a N_1 - d_2 N_2) \end{cases}$	Fungal garden ( $N_1$ )-Leaf cutter ant ( $N_2$ ) Obligate only
Johnson & Amarasekare 2013	S29	$\frac{dN_i}{dt} = N_i \left( r_i + \frac{m_{ij}N_j}{1 + m_{ij}\tau_i N_j + \alpha_i N_i^2} \right)$	Obligate when $r_i < 0$
García-Algarra <i>et al.</i> 2014	S30	$\frac{dN_i}{dt} = N_i (r_i + b_{ij}N_j - (\alpha_i + c_i b_{ij}N_j)N_i)$	Obligate when $r_i \leq 0$
Revilla 2015	S31	$\frac{dN_i}{dt} = N_i \left( r_i + \frac{\sigma_i \beta_i \alpha_j N_j}{\omega_j + \beta_i N_i} - c_i N_i \right)$	Assuming steady-state reward dynamics Exchanges of resources for resources, e.g., Lichens Obligate when $r_i \leq 0$
	S32 S31	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( r_1 + \frac{\sigma_0 \beta_0 \alpha_0 N_0 + \sigma_1 \beta \alpha N_2}{\omega + \beta_0 N_0 + \beta N_2} - c_1 N_1 \right) \\ \frac{dN_2}{dt} = N_2 \left( r_2 + \frac{\sigma_2 \beta \alpha N_1}{\omega + \beta_0 N_0 + \beta N_2} - c_2 N_2 \right) \end{cases}$	Exchanges of resources for services, e.g., Plant ( $N_1$ )-Disperser ( $N_2$ ) Obligate when $r_i \leq 0$
Moore <i>et al.</i> 2018	S34	$\frac{dN_i}{dt} = N_i (r_i + \beta_j N_j - \alpha_i N_i^{\theta_i})$	Accelerating intraspecific density-dependence when $\theta_i > 1$ ; Eqn 1 when $\theta_i = 1$ Facultative only ( $r_i > 0$ )
Cropp & Norbury 2019	S33	$\frac{dN_i}{dt} = N_i \left( r_i \left( \frac{N_j}{\varepsilon_j + N_j} \right) R + a_{ij}N_j - a_{ii}N_i \right)$ where $R = 1 - N_1 - N_2$	Autotrophs ( $N_1$ )-( $N_2$ ) Conservation of mass limits a shared resource $R$ “Obligation” ( $\varepsilon_j > 0$ ) is a separate process from costs & benefits
Wu <i>et al.</i> 2019		Analyzed conditions for system collapse in 81 models of mutualism representing different combinations of saturating benefits due to interspecific density-dependence; zero, linear, or saturating costs due to interspecific density-dependence; and effects of external stress.	
Martignoni <i>et al.</i> 2020	S35 S36	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( r_p + \frac{q_{hp}\alpha N_2}{d + N_1} - q_{cp}\beta N_2 - \mu_p N_1 \right) \\ \frac{dN_2}{dt} = N_2 \left( q_{cm}\beta N_1 - \frac{q_{hm}\alpha N_1}{d + N_1} - \mu_m N_2 \right) \end{cases}$	Plant ( $N_1$ )-Mycorrhizae ( $N_2$ )

Hale <i>et al.</i> 2021	S8	$\frac{dN_2}{dt} = N_2 \left( b_2 + \varepsilon \frac{aN_1}{1 + ahN_1} - s_2N_2 - d_2 \right)$	Set of models for Plants ( $N_1$ , below)- Animal Transporters ( $N_2$ ) Obligate when $b_2 - d_2 \leq 0$
	S37	$\frac{dN_1}{dt} = N_1 \left( \left( b_1 + \beta \frac{aN_2N_1}{1 + ahN_1} \right) g(1 - s_1N_1) - d_1 \right)$	Pollinators increase seed set Obligate when $b_1g - d_1 \leq 0$
	S38	$\frac{dN_1}{dt} = N_1 \left( b_1g \left( 1 - \left( s_1 - \sigma \frac{aN_2}{1 + ahN_1} \right) N_1 \right) - d_1 \right)$	Dispersers reduce negative density-dependence Facultative only
	S39	$\frac{dN_1}{dt} = N_1 \left( b_1 \left( g + \gamma \frac{aN_2}{1 + ahN_1} \right) (1 - s_1N_1) - d_1 \right)$	Dispersers increase germination Obligate when $b_1g - d_1 \leq 0$